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Does the presence of large down wood at the time of a forest fire impact soil recovery?

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ABSTRACT

Fire may remove or create dead wood aboveground, but it is less clear how high severity burning of soils affects belowground microbial communities and soil processes, and for how long. In this study, we investigated soil fungal and bacterial communities and biogeochemical responses of severely burned “red” soil and less severely burned “black” soil from a burned forest on the eastern slope of the Cascade Range in Oregon. Specifically, we examined the effects of burn severity on soil nutrients and microbial communities for 1–4 years after wildfire. Soil nutrients were significantly reduced in red soils. Soil fungi and bacteria, assessed with molecular methods, steadily colonized both burn severities and soil biodiversity increased throughout the study showing that microbial communities seem to have the capacity to quickly adjust to extreme disturbances. Although richness did not vary by soil type, the fungal and bacterial community compositions varied with burn severity. This difference was greatest in the early time points following the fire and decreased with time. However, nutrient-limited conditions of red soils were detected for four years after the wildfire and raise concern about soil productivity at these sites.

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1. Introduction

Frequent, low severity fires historically were characteristic of dry inland forests in the Pacific northwestern region of North America (Heyerdahl et al., 2001). After nearly a century of fire suppression, unprecedented accumulations of plant material on the landscape have contributed to the subsequent increase in large, severe wildfires, challenging forest ecological resilience, particularly in ponderosa pine (*Pinus ponderosa* C. Lawson) forest types (Covington et al., 1997; Savage and Mast, 2005). Studies on prescribed fire and thinning to reduce fuels have been widespread (McIver et al., 2013), but few studies have focused on the soil heating dynamics from downed wood in dry forests (Passovoy and Fulé, 2006; Monsanto and Agee, 2008). Whereas low temperature fire serves to enrich the soil by releasing nutrients bound in accumulated vegetation and litter, intense fire is perceived as a leading cause of soil degradation (Covington et al., 1997; Savage and Mast, 2005). Organic matter is concentrated near the surface of most soil profiles where it is exposed directly to the heat radiated downward during a fire (Neary et al., 1999). Duration of combustion (Neary et al., 1999; Massman and Frank, 2004), soil moisture (Busse et al., 2010), and fuel composition (e.g. large wood) (Busse et al., 2013; Smith et al., 2016) all contribute to temperatures in excess of the lethal threshold for many soil microorganisms. Further, the removal of organic matter by fire significantly affects nutrient content and cation exchange capacity (Korb et al., 2004; Gundale et al., 2005; Bormann et al., 2008; Hebel et al., 2009; Cowan et al., 2016; Ulery et al., 2017) leading to changes in soil functioning.

The presence of large wood is a primary factor leading to high soil temperatures (Busse et al., 2013; Smith et al., 2016). Soils in direct contact with the complete burning of large pieces of down wood or stumps exhibit a distinctive color change where the top layer of mineral soil changes to various shades of red due to excessive heating and oxidation of the soil matrix (Goforth et al., 2005). Severe heating reduces microbial abundance (Bruns et al., 2002; Dahlberg, 2002; Hebel et al., 2009; Peay et al., 2009; Reazin et al., 2016), causes changes in soil chemistry and soil structure (Badía and Martí, 2003; Hubbert et al., 2006; Bormann et al., 2008; Massman et al., 2008; Hebel et al., 2009), and prolongs

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vegetative recovery (Dunn et al., 1985; Guerrero et al., 2005; Bormann et al., 2008; Hebel et al., 2009). Fire burn severity is a qualitative measure that refers to the overall effect of fire on an ecosystem (Neary et al., 1999). The degree of severity can be determined by assessing the physical, chemical, and ecological changes observed post-fire that occur as a direct result of combustion (Keeley, 2009). Burn severity is a product of burn intensity, i.e., the amount of heat energy measured by temperature and duration of heating (NWCG, 2003; Keeley, 2009).

In coniferous forest ecosystems, fungi typically dominate over bacteria (Ananyeva et al., 2006), yet all soil microbes indirectly influence soil productivity in the decomposition of organic matter and through mutualistic symbioses (Wardle et al., 2004). Their role in the cycling of nutrients from organic to inorganic forms, readily assimilated by plants, directly influences the fertility and structure of soil and is essential to maintaining soil health and long-term productivity. Further, the coevolved symbiosis linking mycorrhizal fungi and the roots of plant species unites above and belowground biogeochemical processes and is essential for efficient nutrient acquisition and protection against root pathogens (Courty et al., 2010). Fire influences soil microbial community dynamics and succession, and modifies ecosystem processes in coniferous forests to varying degrees depending on intensity and time since fire (Dahlberg et al., 2001; Dahlberg, 2002; DeLuca et al., 2002). Because soil microbes are ultimately dependent on organic substrates produced through aboveground primary productivity, disturbances such as fire generally have substantial implications belowground (Neary et al., 1999; Hart et al., 2005a, 2005b; Guerrero et al., 2005; Chatterjee et al., 2008).

In the short term, fire significantly reduces soil microbial biomass and in particular, the abundance of fungi (Stendell et al., 1999; Robinson and Bougher, 2003; Smith et al., 2004, 2005). Fungi tend to be less tolerant to heat than bacteria (Bollen, 1969; Guerrero et al., 2005), and in general, burning favors bacteria over fungi (Pietikäinen and Fritze, 1995; D'Ascoli et al., 2005; Bárcenas-Moreno and Bååth, 2009; Hebel et al., 2009). Some fungi have developed mechanisms to survive wildfire and soil heating (Claridge et al., 2009; Peay et al., 2009; Kipfer et al., 2010; McMullan-Fisher et al., 2011; Glassman et al., 2016). For example, spores of post-fire fungi are stimulated by heat or ash to germinate, and commonly start fruiting during the first significant rain event after a fire (Claridge et al.,, 2009).

Knowledge of the impact of severe surface burning on soil microbial communities and soil nutrients is needed to assist forest recovery projects worldwide (Torres and Honrubia, 1997; Cromack et al., 2000; Claridge et al., 2009; Gassibe et al., 2011). Therefore, the aim of our study was to investigate the composition and activity of soil microbial communities in paired severely burned red soil and less severely burned black soil in multiple seasons and years after wildfire. We anticipated that soils beneath the complete combustion of smoldering logs and stumps would be largely void of soil microbes and hypothesized that soil microbial communities would be slow to return to these severely burned sites. Depauperate microbial populations would reduce organic matter turnover and nutrient (nitrogen (N) and phosphorus (P)) mineralization. We investigated the diversity, metabolism, and function of soil fungi and bacteria in relation to soil physicochemical properties in two burn severities immediately after fire and for four years post-fire.

2. Materials and methods

2.1. Study area

This study was conducted within the Booth and Bear Butte (B&B) Fire Complex, located on the eastern slope of the Cascade Mountains of Oregon in the Deschutes National Forest. The Cascade Mountains create a barrier to marine air masses from the Pacific Ocean resulting in the east slope being comparatively drier than the west slope. Stands in the study belong to the *Abies concolor – Abies grandis* plant classification series as described by Simpson (2007) with Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) or ponderosa pine or both, typically dominating the overstory canopy. White fir (*Abies concolor* Gord. & Glend., Lindl. Ex Hildebr.) and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) are less fire resistant than ponderosa pine or mature Douglas-fir, and historically were removed or reduced in stands by frequent fire (Agee, 1993). The proportional increase of white fir and grand fir has increased ladder fuels and the threat of stand-replacing wildfires. An understory of snowbrush ceanothus (*Ceanothus velutinus* Dougl.), dwarf rose (*Rosa gymnocarpa* Nutt.), common snowberry (*Symphoricarpos albus* [L.] Blake), dwarf Oregon grape (*Mahonia nervosa* [Pursh] Nutt.), trailing blackberry (*Rubus ursinus* Cham. & Schlecht) and red huckleberry (*Vaccinium parvifolium* Sm.) occurs on our stands. Soils are 79 cm in depth (to bedrock) and are classified as Aquic Vitrixerands and Alfic Vitrixerands with sandy-loam texture (http://websoilsurvey.nrcs.usda.gov/app/help/citation.htm). Elevations range from 900 to 1350 m (Table 1). Average temperatures range from −1 °C in the winter months to 20 °C in the summer months. Average annual precipitation ranges from 500 to 1500 mm. About 70% of the precipitation falls during November through April. During the driest months (July, August, and September), the average monthly precipitation is less than 25 mm.

The B&B Fire burned 36,733 ha in August of 2003. The fire was of mixed severity but based on satellite imagery, a substantial percentage (~32%) burned with high mortality resulting in stand replacement (USDA, 2005). While fire is a natural part of the forest landscape and disturbance regime, the B&B fire was uncharacteristic in size and mortality of trees, particularly in lower elevations, compared to fires of the previous 100 years (USDA, 2005). In general, severely burned soils, measured with transects and polygons, ranged from trace amounts to ~6%, with 1–3% the norm (Shank, 2004). However, in areas that contained large down wood from 1987 fires, the percentage of red soil occupied ~19% of the landscape investigated (Shank, 2004).

2.2. Study design and sampling

In October 2003, immediately after containment of the B&B fire and prior to rainfall that may have induced soil movement, preliminary soil sampling for fungal richness occurred at 3 sites containing red and black soil from each of 2 stands (blocks) within the Jefferson Wilderness, Deschutes National Forest. Ten additional preliminary samples were collected from 10 red soil locations. In spring 2004, the study was expanded to include a total of 5 stands within the perimeter of the fire where significant percentages of severely burned soils accompanied significant tree mortality due to stand replacing wildfire. Stands were each ~10 ha in size. At each of the 5 stands, 3 sites were established that each included a red soil plot and adjacent (<2 m distance) black soil plot similar in size to the paired red plot (Table 1). As described in Hebel et al. (2009), red soil plots were commonly found as linear strips ≤1 m wide and ≥3 m long, that were created as downed logs were consumed by fire, but also occurred as deep, irregular patches often 90 cm or more in diameter, where stumps and root systems were consumed by fire. Depth of the red soil layer in our plots exceeded 5 cm and averaged ~10 cm. Sites within a stand were at least 200 m apart. In spring 2006, partial logging of stand 1210 eliminated site 3, reducing the number of sites in this stand to 2 for the remainder of the study. Soil samples to determine fungal richness were collected in spring, summer, and fall of 2004, 2005, 2006, and in spring 2007, for a total of 10 seasons. Funding

Table 1
Stand elevations and locations within the Booth and Bear Butte (B&B) Fire complex, located on the east side of the Cascade Mountains of Oregon in the Deschutes National Forest. Paired red and black soil samples were collected from adjacent plots (<2 m apart) at each location.

Stand	Site	Elevation (m)	Location
BH	1	979	N44°33′41, W121°40′55
	2	983	N44°33′44, W121°40′53
	3	971	N44°33′45, W121°40′52
LJ	7	1030	N44°35′11, W121°41′47
	10	1020	N44°35′12, W121°41′31
	12	990	N44°35′18, W121°41′18
UJ	1	1107	N44°35′35, W121°41′88
	3	1068	N44°35′37, W121°41′79
	5	1059	N44°35′35, W121°41′75
1210	1	1349	N44°26′24, W121°45′81
	2	1340	N44°25′95, W121°45′82
	3	1336	N44°26′05, W121°45′73
1280	1	913	N44°32′67, W121°40′28
	3	925	N44°32′69, W121°40′33
	5	922	N44°32′73, W121°40′35

for the project in 2005 allowed for measurement of additional response variables including bacterial richness, initiated in the summer of 2005. Additional response variables were selected based on their ability to influence soil fungi and bacteria and their processes.

Three representative sampling locations were selected at each plot. A sparse layer of fallen tree needles was gently removed and the top 5 cm of mineral soil was collected with a garden trowel and combined and thoroughly mixed in a plastic bag to create a composite plot-scale soil sample. Rocks and plant material (roots and needles) were removed from the composite soil samples before being divided into aliquots for molecular and chemical analysis. Soil samples were transported to the lab on ice and stored at −80 °C for molecular analysis, and at 4 °C for soil chemical and physical analysis.

Soil respiration data for spring, summer, and fall of 2005 and 2006 were obtained (Law et al., 2001) using a LI6200 infrared gas analyzer (LiCor, Lincoln, NE, USA). Soil respiration rates were expressed as $\mu\text{mol m}^{-2}\,\text{s}^{-1}$ of CO_2, using the same convention and quantification as Sulzman et al. (2005).

2.3. Soil physical properties

Soil strength was measured at each plot in the fall of 2005 using the Rimik 4011 recording soil penetrometer (Rimik International Pty Ltd, Queensland, Australia) at 2.5 cm increments. Five measurements at each plot were taken to a maximum depth of 60 cm. Bulk density (soil core) was assessed in the fall of 2005 (0–5 cm) and the springs of 2006 (5–10 cm) and 2007 (0–5 cm, 5–10 cm). Gravimetric water content (% moisture) was measured in each plot in spring, summer, and fall of 2005 and 2006 to calculate water-filled pore space, an attribute critical to mass flow of nutrients, as well as to limits to biological activity.

2.4. Soil chemistry and mineralizable (anaerobic incubation) N

Chemical analysis was performed on mineral soils collected during each summer sampling period including mineralizable (anaerobic incubation) N in summer 2004 and 2007. In the laboratory, soil samples were sieved (2.0 mm) and air-dried. All soil chemistry analyses were conducted at the Oregon State University Central Analytical Lab using methods detailed in Horneck et al. (1989). Soil samples were analyzed for total C (Nelson and Sommers, 1996) and total N (Bremner, 1996) by the dry combustion technique using a Flash EA112 NC soil analyzer (Thermo Electron Corporation, Milan, Italy); cation exchange capacity (CEC) (c $\text{mol}_c\ \text{kg}^{-1}$) was estimated using the sum of exchangeable cations (Robertson et al., 1999); soil pH by the 1:2 (soil:water) dilution method using deionized water (Robertson et al., 1999); and plant available P (as Bray P) ppm by the dilute acid-fluoride method (Kuo, 1996). Anaerobic incubation N (NH_4-N) (ppm) was measured using the procedure of Bundy and Meisinger (1994). After incubation at 40 °C for 7 days, 50 ml of 2 M KCL was added, placed on a mechanical shaker for 1 h to extract NH_4–N. The indophenol blue method with salicylate was used to quantify NH_4 with an Alpkem rapid flow analyzer (RF-300), (Astoria-Pacific, Clackamas, OR).

2.5. Molecular analysis of samples

A MoBio Power Soil™ DNA isolation kit was used to extract total genomic DNA from approximately 0.5 g of homogenized soil from each sample (MoBio Laboratories, Carlsbad, CA, USA). Soil fungi DNA was amplified using ITS1F and ITS4 (FAM) (Gardes and Bruns, 1993). Each soil DNA extract was PCR amplified twice following the methods of Dickie et al. (2002). Once amplified, the two products were pooled to more fully capture the diversity. These pooled products were then purified using a MoBio Ultra Clean DNA Clean Up kit (MoBio Laboratories, Carlsbad, CA). Both *Hinf*I and *Hae*III restriction enzymes are widely used in fungal terminal restriction fragment length polymorphism (T-RFLP) profiling (Avis et al., 2006); however, *Hinf*I was selected over *Hae*III for our study after comparison trials on replicate samples revealed its ability to identify the greatest amount of variation. Similar methods were followed to identify soil bacteria communities; DNA extracts were PCR amplified using 16S rDNA gene primers 8F (FAM) and 907R (Muyzer et al., 1995) following the methods described by Jennings et al. (2012). Amplicons were digested using the restriction enzyme *Msp*I. All restriction digests were performed according to the manufacturer's specifications (Promega, Madison, WI) and restricted samples were submitted to Oregon State University Center for Gene Research and Biotechnology (CGRB) for analysis using an ABI Prism 3100 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA, USA) to run capillary gel electrophoresis. Genemapper software 4.0 (Applied Biosystems Inc., Foster City, CA) was used to determine fragment fluorescence and bin peaks into operational taxonomic units (OTUs). OTUs, practical proxies for microbial species (Moeseneder et al., 1999), show a general agreement in assemblage composition, distribution patterns, and relationships with environmental variables (Santoferrara et al., 2016). Peak area was normalized by total fluorescence of each sample and used as a proxy for relative abundance in community matrices. Matrices were de-noised by removing OTUs comprising less than 1% of the total fluorescence in a sample and OTUs present in only one sample.

Fifty-three samples were selected to produce fungal clone libraries. Selection was based on the complexity of the TRF profile, obtaining an approximately equal number of samples from red and black soils, and representation of most sample times. These criteria resulted in 28 samples from red soils and 25 from black soils, and two to nine samples from each sample time except spring 2005 in which no samples were selected (Suppl. Table 1). Soil DNA extracts were amplified with ITS1F and ITS4 primers (see above for details) followed by ligation of the amplicons into the pCR®4 TOPO TA cloning vector (Invitrogen, Carlsbad, CA, USA) and transformation into TOP10 chemically competent *Escherichia coli* cells according to the manufacturer's directions. Transformants were re-amplified with ITS1F and ITS4 and subsequently sequenced directly using ABI Prism® BigDye™; (Applied Biosystems, Foster City, CA, USA) and an automated ABI Prism® 3700 DNA Analyzer (Applied Biosystems) at the Oregon State University CGRB.

2.6. Statistical analyses

The structure of this study for soil attributes measured in only one year is a generalized random block design with replicated and paired treatments. When measurements were made through time (more than one season and year), the structure is a generalized random block design with replicated and paired treatments with repeated measures and were analyzed using a univariate split-plot structure. All analyses were performed using the PROC MIXED procedure in SAS computer software (SAS Institute, 2002–2005). For most seasons of the study, there were 5 stands with 3 sites containing two soil severities, for a total of 30 plots.

The mean responses for soil properties were compared among treatments, and when appropriate, among seasons and years. Interactions, when significant, are reported. Results were considered significant at $P \leq 0.05$. The F statistic and P-value are presented in the text when not included in a table.

Multivariate analysis of fungal and bacterial T-RFLP community profiles was performed in the vegan package (Oksanen et al., 2015) for R statistical software (R Core Team, 2014). The “vegdist” function was used to calculate the Bray-Curtis distance on fungal and bacterial community matrices. Principal coordinate analysis (PCoA) ordinations were constructed using the “cmdscale” function and “envfit” was used to evaluate significant correlations between soil biogeochemical properties and community structure. PERMANOVA analysis was used to determine the effect of site, sampling date, soil type, and their interactions on community composition using the “adonis” function.

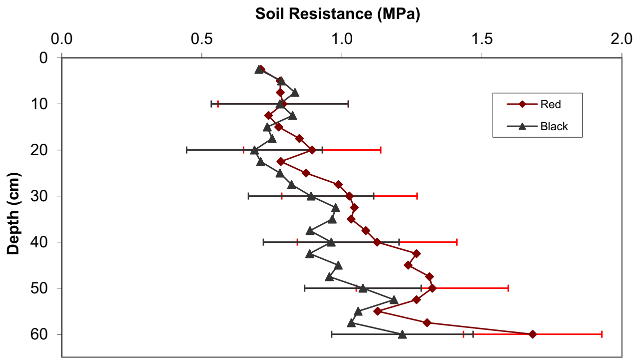

Fig. 1. Soil strength measurements by soil burn severity. Measurements were taken at 2.5 cm increments to a depth of 60 cm. Soil strength (compaction) did not differ between the red and black soils, but penetrometer measurements (Rimik 4011, Rimik International Pty Ltd, Queensland, Australia) revealed a trend suggesting greater soil strength in the red soils at depths greater than 15 cm. Error bars represent 1 SE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Soil physical properties

Soil strength (compaction) did not differ between the red and black soils, but penetrometer measurements revealed a trend suggesting greater soil strength in the red soils at depths greater than 15 cm (Fig. 1). Bulk density at 5 cm and 10 cm did not differ between red and black soils (Table 2). Although percent moisture was up to 85% lower in summer compared with fall and spring (95% CI = 76–99%, 95% CI = 73–99%, respectively) ($F_{[2,130]} = 157.71$, $P < 0.0001$), a difference in percent moisture between red and black soils was not observed ($P = 0.29$) (Table 2).

3.2. Soil chemistry, mineralizable (anaerobic incubation) N, and soil respiration

All chemical and biochemical analyses showed significant differences between the two burn severities (Table 2). Soil pH was highest in red soil, while CEC, plant-available P (Bray), total C and N, and anaerobic incubation NH_4–N all were highest in black soil. Temporal and interaction responses are displayed in Fig. 2. Total C did not differ by year but showed a treatment by year interaction ($F_{[3,70]} = 17.88$, $P < 0.0001$) due to total C declining then stabilizing in black soils in contrast to being largely depleted and increasing in red soils over time. Accordingly, CEC differed by year ($F_{[3,69]} = 6.08$, $P = 0.001$) and displayed a treatment by year interaction ($F_{[3,69]} = 4.48$, $P = 0.006$) attributed to CEC declining in black soils and increasing in red soils over time. Total N differed by year ($F_{[3,67]} = 43.03$, $P < 0.0001$) with a treatment by year interaction ($F_{[3,67]} = 10.32$, $P < 0.0001$) probably due to a larger divergence in 2004 than in subsequent years. Mineralizable N increased in both red and black soils from 2004 to 2007 ($F_{[1,18]} = 16.10$, $P = 0.0008$). Available P ($F_{[3,70]} = 8.94$, $P < 0.0001$), C/N ratio ($F_{[3,66]} = 66.80$, $P < 0.0001$) and pH ($F_{[3,70]} = 21.70$, $P < 0.0001$) all showed significant temporal variation without an interactive treatment effect.

Soil respiration rates did not differ with respect to soil burn severity ($F_{[1,24]} = 0.45$, $P = 0.51$), but did differ by season ($F_{[2,134]} = 197.76$, $P < 0.0001$) (Table 2, Fig. 2h). Soil respiration rates were, on average, more than 38% lower in fall compared to spring or summer.

Table 2
Effects of burn severity on soil biogeochemical response variables. Means are listed with standard errors in parentheses. The F statistic is testing the null hypothesis of no difference between the two soil burn severities. Means differing at $\alpha = 0.05$ are shown in bold. The data in the nonburn column are provided for reference only and are from a nearby nonburned area within the perimeter of the B&B fire; samples were collected from Summer 2005 – Summer 2007 as part of a logging effects study (Jennings et al., 2012).

Soil response variable	Severity				
	Red	Black	Nonburn	$F_{[df,df]}$	P
Bulk Density at 5 cm depth ($g\ cm^{-3}$)	0.98 (0.02)	0.96 (0.03)	0.83 (0.06)	$0.53_{[1,20]}$	0.48
Bulk Density at 10 cm depth ($g\ cm^{-3}$)	0.90 (0.04)	0.91 (0.04)	0.98 (0.03)	$0.03_{[1,19]}$	0.87
Moisture (%)	18.34 (1.55)	19.55 (1.50)	17.49 (2.24	$1.15_{[1,24]}$	0.29
CEC ($c\ mol_c\ kg^{-1}$)	13.87 (0.85)	19.42 (0.86)	15.47 (1.12)	$71.63_{[1,24]}$	**<0.01**
pH	7.51 (0.05)	7.08 (0.068)	6.56 (0.06)	$27.28_{[1,24]}$	**<0.01**
C:N	18.09 (0.84)	20.78 (0.73)	20.92 (2.01)	$22.47_{[1,24]}$	**<0.01**
Total C ($g\ kg^{-1}$)	15.90 (1.10)	30.70 (1.20)	27.99 (2.38)	$93.42_{[1,24]}$	**<0.01**
Total N ($g\ kg^{-1}$)	1.00 (0.10)	1.60 (0.10)	1.41 (0.17)	$55.67_{[1,24]}$	**<0.01**
Available P (P-Bray) ($mg\ kg^{-1}$)	8.94 (1.26)	16.55 (2.07)	9.67 (1.72)	$15.96_{[1,24]}$	**<0.01**
Anaerobic incubation NH_4–N ($mg\ kg^{-1}$)	25.45 (4.28)	39.51 (3.83)	29.23 (5.76)	$8.33_{[1,22]}$	**<0.01**
Mean # fungal OTUs (*Hinf*I)	17.76 (1.72)	17.72 (1.72)	20.29 (1.38)	$0.00_{[1,4]}$	0.98
Mean # bacterial OTUs (*Msp*I)	25.70 (1.29)	26.70 (1.29)	24.43 (0.99)	$1.67_{[1,4]}$	0.27
Respiration ($\mu mol\ m^{-2}\ s^{-1}$)	2.12 (0.15)	2.01 (0.12)	3.11 (0.24)	$0.45_{[1,24]}$	0.51

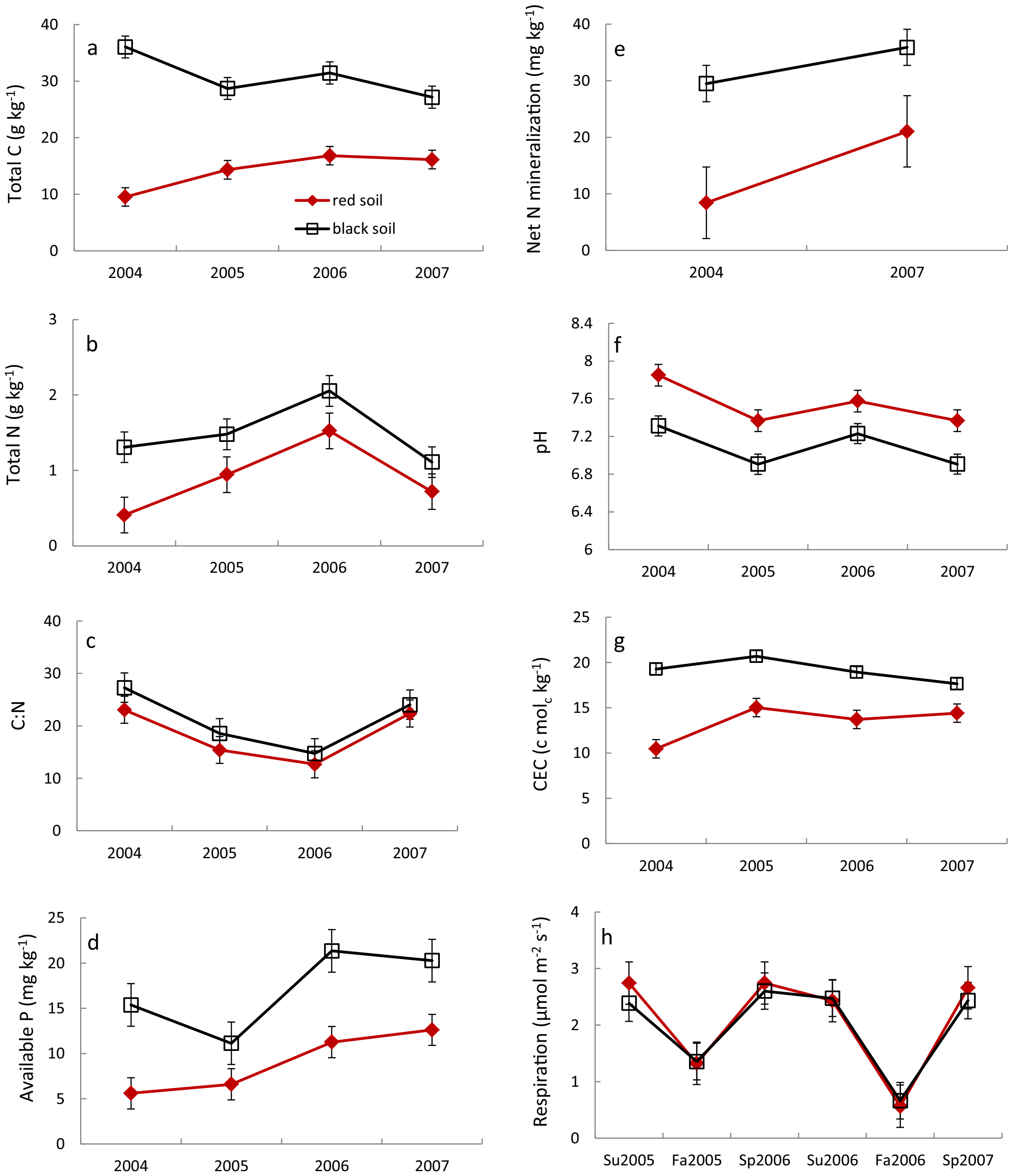

Fig. 2. Means and standard errors of soil chemical, biological, and biochemical response variables for the two burn severities. (a) Total Carbon (C), (b) Total Nitrogen (N), (c) C:N, (d) Available (Bray) Phosphorus (P), (e) net N mineralization, (f) pH, (g) Cation Exchange Capacity (CEC), (h) respiration. Error bars represent 1 SE.

3.3. Soil microbial communities

Results from our exploratory preliminary sampling seven weeks post fire indicated the presence of fungi in all 6 black soils and in 12 of 16 red soil samples (data not shown). As expected, these samples were relatively low in richness with only six OTUs detected in red soil, three in black soil. One OTU was particularly ubiquitous and detected in 11 of the 12 paired plots and was the only OTU in the additional red soil samples, unfortunately, we were unable to identify this OTU by comparing the T-RF to the clone library taxa.

Both soil types showed a gradual increase in the cumulative number of fungi and bacteria with each sample time (Fig. 3). Overall, fungal T-RFLP profiles had a total of 163 OTUs (Fig. 3); there was no difference in the mean number of fungal OTUs between treatments ($F_{[1,4]} = 0.00$, $P = 0.98$), although differences were detected among sampling periods ($F_{[9,68]} = 15.98$, $P < 0.001$) with the greatest number occurring in spring 2007 (Fig. 4). A total of 161 bacterial OTUs (Fig. 3) were detected. As with the fungi, there was no difference in the mean number of bacterial OTUs between treatments ($F_{[1,4]} = 1.67$, $P = 0.27$), although the difference among sampling periods ($F_{[5,40]} = 2.34$, $P = 0.06$) was weaker than for fungi.

Both bacterial and fungal community structure separated on the first two dimensions of the PCoA ordinations (Fig. 5). Samples taken closer to the time of the fire (represented as smaller points in the ordination) show distinct differences between black and red soils, and communities become more similar with time (increasingly larger points). This trend was confirmed with PERMANOVA

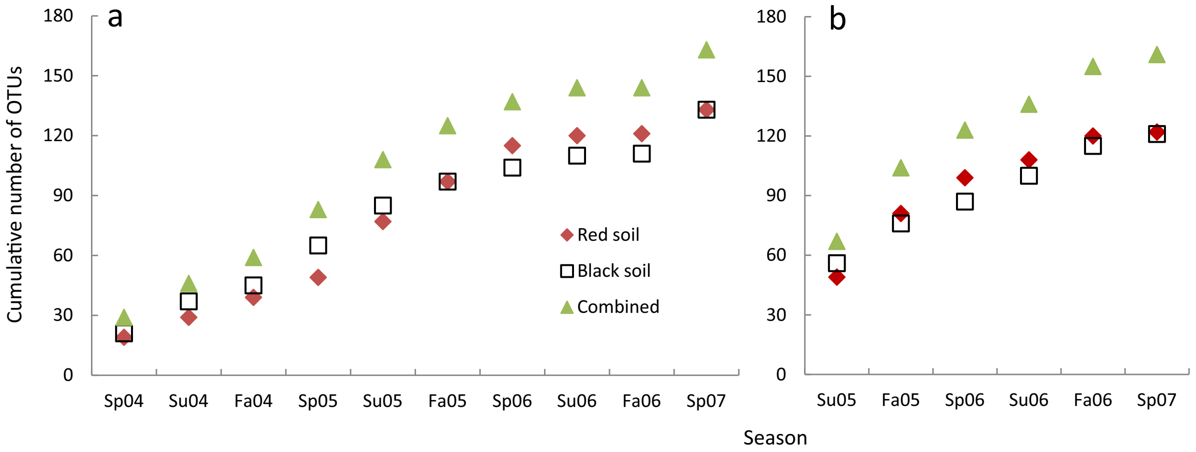

Fig. 3. Cumulative number of (a) fungal (*Hinf*I) OTUs and (b) bacterial (*Msp*I) OTUs by season and year for red soil, black soil, and combined. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

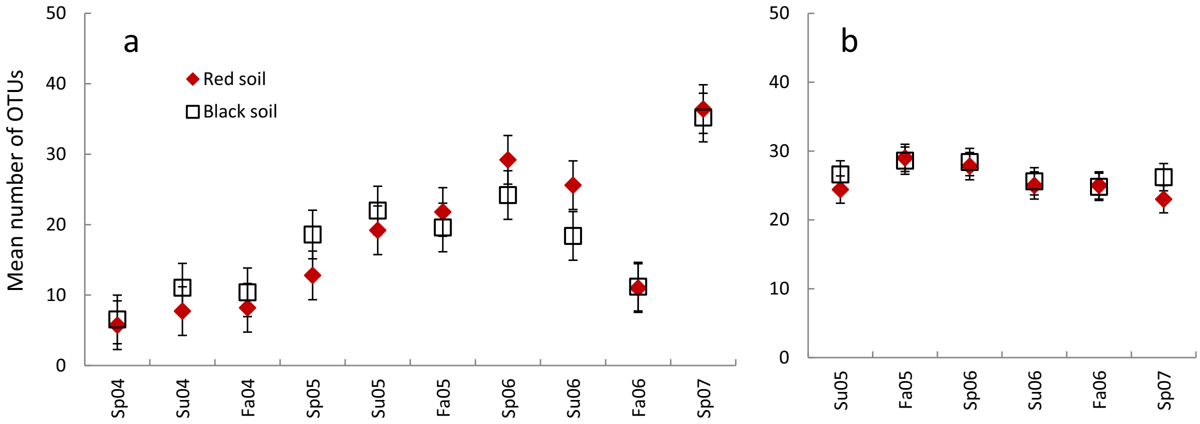

Fig. 4. Mean number of (a) fungal (*Hinf*I) OTUs and (b) bacterial (*Msp*I) OTUs by season and year for red soil, black soil. Error bars represent 1 SE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

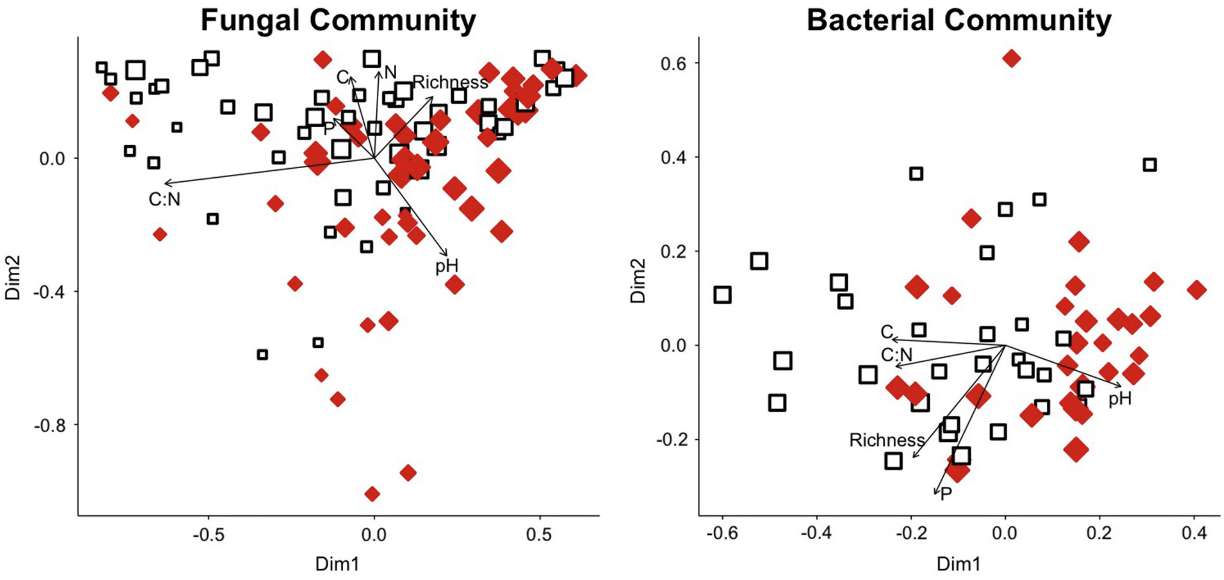

Fig. 5. Principal coordinate analysis of fungal and bacterial communities. Analysis based on relative abundance of T-RF fragments using Bray-Curtis distance measure. Solid red diamonds and open black squares represent red and black soils, respectively. Relative size of the point indicates sampling date with smaller points representing samples taken closer to the time of burn and increasing in size with time since the burn. Biplot vectors represent significant ($p < 0.05$) environmental variables. To improve figure clarity, points represent mean values for PCoA scores for plots within a stand. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

results indicating significant differences between soil types, time points, and their interaction ($p < 0.01$ for each term in both fungal and bacterial communities). Environmental variables that are significantly correlated with community composition ($p < 0.05$) are represented with vector overlays with vector length scaled to respective R^2 values. Soil pH is strongly correlated with the structure of both the fungal and bacterial communities, and the vector direction indicates that communities from recently burned soils are associated with a higher pH. Conversely, fungal and bacterial communities from black soils were associated with vectors for C, N, and C:N. The vector for community richness did not appear to correlate with soil type, but rather with sampling time, which is congruent with results presented in Figs. 3 and 4.

Clone libraries from the 53 soil samples resulted in a total of 883 sequences representing 118 Ascomycota, 56 Basidiomycota, 23 Chytridiomycota, and 9 Zygomycota taxa. Cloning results for these phyla are displayed by soil burn severity and sampling time in Suppl. Table 1. Cloning of two each of the initial samples from fall 2003 revealed seven OTUs, (two *Pyronemas* from red soil, and two *Pyronemas*, a Pezizomycetes, an Ascomycota, and *Lyophyllum* from black soil). Ascomycota sequences consistently outnumbered the Basidiomycota in all but one sample time (fall 2006). The Chytridiomycota were detected in 90% (9/10) of the sampling times in both red and black soils and were particularly abundant in the final (spring 2007) sample time when they accounted for 18% (27/152) of the taxa. The Zygomycota were not detected until spring 2006 at which time they were detected in both the red and black soils. Persistence over multiple sampling seasons at a localized scale was observed for the majority of fungal taxa and most were detected within a single soil burn severity plot in two sampling seasons (Suppl. Table 1). Examples of repeated detection at the plot scale were seen in all four phyla.

4. Discussion

4.1. Soil microbial communities

We detected few fungal species in the preliminary samples collected immediately after fire suggesting that temperatures lethal to soil microbes occurred in both red and black soils. Temperatures in the range of 50–80 °C are considered lethal for most soil inhabiting fungi and most soil organisms are killed at temperatures between 50 and 120 °C (Dunn et al., 1985; Neary et al., 1999; Guerrero et al., 2005). Lethal temperatures to depths of 5 to 10 cm are common in a variety of burn conditions and fuel types including in clear-cut areas originally supporting jack pine (*Pinus banksiana* Lamb.) (Sims, 1976), in dry soil beneath masticated forest residue (Busse et al., 2005, 2010) and beneath log and slash piles (Massman and Frank, 2004; Jiménez Esquilín et al., 2007; Busse et al., 2013; Smith et al., 2016). Despite high temperatures in the upper soil profiles, forest soils are insulating and temperatures exponentially decline with soil depth (Massman and Frank, 2004; Busse et al., 2010, 2013; Smith et al., 2016).

Following severe forest ecosystem disturbances such as stand-replacing wildfire, soil biota are essential for the re-establishment of soil biogeochemical processes that contribute to forest recovery (Coleman et al., 1992; Wardle et al., 2004; van der Heijden et al., 2008). Contrary to our hypothesis, no difference in the mean number of fungal or bacterial OTUs between soil burn severity type was detected (Figs. 3 and 4, Table 2), although soil fungi and bacteria steadily colonized both soil burn severities and increased soil biodiversity over time (Fig. 3). Our findings support those of Kageyama et al. (2013), Cowan et al. (2016) and Reazin et al. (2016) showing that microbial communities seem to have the capacity to quickly adjust to extreme disturbances. Most OTUs detected in our study occurred in both red and black soils (Fig. 3) and many of the early inhabitants persisted through time. About 75% of the fungal OTUs detected in the first sample season (spring 2004) were detected in later seasons. Similarly, a majority (61%) of the bacterial OTUs were detected throughout the study. Although richness did not vary by soil type, the fungal and bacterial community compositions varied with burn severity. This difference was greatest in the early time points following the fire and decreased with time (Fig. 5). By spring 2007, nearly four years post-burn, red and black soils had similar microbial community compositions indicating that although fungal and bacterial communities are impacted by burn severity, they can recover to a similar post-fire state. Our study provides knowledge about the succession and persistence of soil microbes in burned soils but we acknowledge that our experimental design did not allow us to address whether the trends in fungal and bacterial communities resemble a pre-burn or unburned state.

Reazin et al. (2016) also show that fires of differing intensities rapidly select distinct microbial communities and suggest that return to pre-burn states may be a slow process. Recovery to a pre-disturbance community state required more than a decade in soils subjected to a long-term prescribed burn regime in coniferous stands on the Piedmont of central Georgia (USA)(Oliver et al., 2015), in a fire chronosequence study in Alaskan boreal forests (Holden et al., 2013), and in meta-analysis by Dooley and Treseder (2012). Continued monitoring of microbial communities in soils receiving different fire intensities will further understanding of microbial succession after disturbance.

4.2. Soil biochemical properties

Studies in pine forests have shown noticeable effects of fire on nutrient availability in the upper 5 cm (Prieto-Fernandez et al., 1993; Monleon et al., 1997) and fires of lower severity and thus lower heat penetration into mineral soil result in significantly lower losses of labile N compared to high severity fires (Choromanska and DeLuca, 2001). The loss of organic matter in red soil resulted in 54% less soil C to a depth of 5 cm than in black soil. Similarly, in red soils total N was 40% less and plant available P was 47% less than in black soils. The initial low level of total N in the red soils corresponded with a sharp increase in net N mineralization with time as organic matter accumulated and total N and soil microbes increased (Fig. 2). Net N mineralization in the black soils mimicked this increase, albeit less dramatically. Nitrogen mineralization potential, the conversion of organic N in microbial biomass to inorganic N under laboratory conditions, is considered a potential estimate of biologically available N (Myrold, 1987). Initial and early increases in total N in both red and black soils are likely attributed to heat-killed microbial tissues and heat disrupted soil organic matter (Pietikäinen and Fritze, 1993; Choromanska and DeLuca, 2001, 2002; Cowan et al., 2016), as well as a steady increase in pioneering soil fungi and bacteria.

Substrate changes induced by heat may select for fungi that tolerate a high pH or may enhance hyphal growth and fruiting (El-Abyad and Webster, 1968; Petersen, 1970; McMullan-Fisher et al., 2011; Glassman et al., 2016). The rapid growth rate of pyrophilous fungi, permitting them to fill open niches ahead of slower growing species, likely contributes to soil respiration rates and may partially explain why a difference in respiration was not detected between our red and black soils. A similar pattern in soil respiration and mean fungal taxa (Figs 2h and 4) suggests that fungi more directly contributed to CO_2 efflux than bacteria, whose taxa pattern showed little seasonal fluctuation. Soil respiration is a direct measure of both microbial and root activity so it is surprising that respiration rates between red and black soils did not differ despite 51% less vegetative cover on our red soil plots than black soil plots 2 years post fire (Hebel et al., 2009) when respiration was first measured.

4.3. Fungal succession and ecosystem function

Fungal clone libraries were dominated by Ascomycota, the largest phylum of Fungi. Because we undertook a representational approach to selecting samples for cloning, it is not possible to directly compare taxa composition between the soil burn severities. Nevertheless, commonalities and inferences can be drawn. Ascomycota tend to colonize earlier in succession than Basidiomycota (Rayner and Boddy, 1997) and throughout the sample times in our study, Ascomycota typically outnumbered the Basidiomycota by two to three times. Reazin et al. (2016) report a substantial soil community turnover and corresponding replacement of the dominant basidiomycetes by ascomycetes, particularly after high intensity fire. Kurth et al. (2013) also report Ascomycota dominance in the community structure of wood-inhabiting fungi in ponderosa pine forests after wildfire.

A majority of the detected Ascomycota taxa are in the Pezizales. Soil-inhabiting Pezizales often occur on burnt ground and have a preference for high pH and low content of organic matter (Petersen, 1985; Fujimura et al., 2005; Hansen et al., 2013) making them well suited to the slightly alkaline (pH 7.5) red soils. Many of these pioneering species have been considered to be saprobic; however an increasing number have been identified as ectomycorrhizal associates (Tedersoo et al., 2006; Hansen et al., 2013), including *Geopyxis* and *Morchella* (morels) (Buscot and Kotte, 1990; Vrålstad et al., 1998; Dahlstrom et al., 2000) although isotopic evidence suggests saprotrophy for post-fire *Morchella* in Oregon (Hobbie et al., 2016).

Although Ascomycota dominated immediately post-fire, Basidiomycota were also present. Notably, *Lyophyllum* was detected in the preliminary fall 2003 sampling as well as in the first spring sampling. Early sporocarp production by this fungus occurred in Mediterranean forests where tree and understory vegetation were totally destroyed by fire (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013). *Basidioascus* and Geminibasidiaceae were detected throughout our study, lending support that they are widely distributed in soil (Nguyen et al., 2013), and contributing to the scant knowledge about heat-resistant basidiomycete taxa (Bollen, 1969, 1974; Izzo et al., 2006; Peay et al., 2009; Kipfer et al., 2010; Nguyen et al., 2013). An increasing number of ectomycorrhizal Basidiomycota, including *Rhizopogon*, Sebacinales, Thelephorales, and *Tomentella*, were found throughout the study. A simplification of the ectomycorrhizal assemblage structure after fire with persistence of *Rhizopogon* and *Wilcoxina* has been repeatedly shown in field studies (Horton et al., 1998; Stendell et al., 1999; Fujimura et al., 2005; Smith et al., 2004, 2005; Cowan et al., 2016; Glassman et al., 2016) and controlled soil heating studies (Izzo et al., 2006; Peay et al., 2009; Kipfer et al., 2010). Although these taxa were not present in our clone libraries during the early seasons of our study, ponderosa pine seedling bioassays confirmed their presence one year after the burn (Jennings and Smith, unpublished data).

Chytridiomycota (chytrids) were detected throughout the study beginning in the first spring sample time (Suppl. Table 1). Chytridiomycota, the only phylum of true Fungi that reproduces with motile spores (flagellated zoospores), occur predominantly as saprophytes in terrestrial habitats including forest soils where they degrade recalcitrant materials such as pollen grains, chitin, keratin, and cellulose (Letcher and Powell, 2001; James et al., 2006). Some soil-inhabiting chytrids recover from drying and temperatures of −90 °C (Gleason et al., 2004, 2005).

4.4. Soil physical properties

Thermally altered reddened soil surfaces are common in Mediterranean-type climate regions after forest fires in places where logs have combusted on the ground surface (Ulery and Graham, 1993; Shank, 2004; Goforth et al., 2005; Ulery et al., 2017). Intense burns consume organic matter that binds soil particles into aggregates potentially leading to loss of soil structure, increased bulk density and reduced soil porosity (Neary et al., 1999; Hubbert et al., 2006). However, we did not detect a difference in bulk density or soil strength values (Fig. 1) between red and black soils.

4.5. Implications for forest management

The extremely nutrient-limited conditions of red soils persist years after fire, and raise concerns about soil productivity. Fire severity also had a significant influence on soil microbial communities and although soil communities became more similar with time, it's difficult to determine how this lag may influence biogeochemical processes and forest recovery. Despite the differences between red and black soils in soil nutrients and microbial communities, we observed a surprising amount of similar characteristics between soil types including bulk density, strength, C:N, respiration, and bacterial and fungal species richness.

Within stands of high mortality the extent of extreme soil burning from down wood is localized and red soil conditions may be of minor consequence because of their typical infrequence (Goforth et al., 2005; Ulery et al., 2017). Within most of the B&B Fire perimeter, red soils occupied $\leq$6% of the land surface (Shank, 2004). However, in areas of the B&B Fire that contained large down wood from 1987 fires, red soil conditions were observed on $\sim$19% of the forest floor (Shank, 2004). As burned areas continue to increase across U.S. western forests (Stephens, 2005; Attiwill and Binkley, 2013), incorporating previously burned areas into management plans and understanding the temporal fuel dynamics following high-severity fire will be essential (Dunn and Bailey, 2015).

Snag stems and large branches are the primary source of 1000-h fuels following wildfire (Dunn and Bailey, 2015). Thus, it is important to consider the desired future forest ecosystem structure, and whether post fire intervention such as the recurrent use of fire (Dunn and Bailey, 2015) or logging (Turner et al., 1998; McIver and Ottmar, 2007; Buma and Wessman, 2011) may mitigate the potential conversion from forest to non-forest in the event of a future fire. Considerable controversy and uncertainty about the outcomes of post fire management on ecological recovery prevail and interactions between multiple disturbances have potential for long-lasting legacies on landscape structure and function (Buma and Wessman, 2011; Dillon et al., 2011). Lack of seedling recruitment in areas that experienced non-typical high severity fire and higher regeneration densities in salvage logged treatments lends support to post fire harvest as a restoration strategy (Buma and Wessman, 2011). In an area salvage logged after the B&B Fire, plant available N in soils compacted by mechanical application was about 50% greater than plant available N in our red soils; plant available P and microbial species richness were comparable to those in our red soils (Jennings et al., 2012). Post fire logging however, has been implicated with increasing the risk of fire and hindering regeneration (Donato et al., 2006; Thompson et al., 2007) and decreasing the amount of C for long-term storage (DeLuca and Aplet, 2008; Mitchell et al., 2009).

Where past fire suppression has contributed to an increase in fire severity, (e.g. ponderosa pine forest types), large severe fires are generally considered deleterious (Covington et al., 1997; Savage and Mast, 2005). In contrast, infrequent, large severe fires in lodgepole pine (*Pinus contorta* Douglas ex Loudon *var. latifolia*

Engelm. ex S. Watson) and high-elevation spruce–fir (*Picea–Abies*) are considered a natural disturbance process recognized as determinants of ecosystem structure, function, and composition (Turner et al., 2003; Noss et al., 2006; Schoennagel et al., 2008). Disparate ecosystem responses emphasize the need for scrutiny and thoughtful interpretation of fuel reduction practices and their effects on soil quality (Reynolds et al., 2011).

Forest wildfires contribute to landscape heterogeneity by creating a mosaic of disturbance depending on the variation of fuel load (Schoennagel et al., 2008). The diversity of ecosystem types, soils, fuels, fires, land use, and climate conditions suggest caution in developing generalizations and highlight the importance of knowledge originating from local and traditional understanding of how these factors interact across a landscape (Boyd, 1999; Brown et al., 2003; Boerner et al., 2009; Busse et al., 2014). How ecosystems respond to high severity fire, and in what timeframe, will require further understanding of how different forest ecosystems are adapted to typical, atypical, and multiple disturbances including climate change. Continued monitoring of severely burned red soils and soils in salvage logged stands will provide insight about cumulative effects of these impacts on post-fire ecosystem recovery.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.02.013.

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